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Research

Population responses to observed climate variability across multiple organismal groups

Christie Le Coeur, Jonathan Storkey and Satu Ramula

C. Le Coeur (https://orcid.org/0000-0002-0911-2506) ✉ (christielecoeur@gmail.com) and S. Ramula (https://orcid.org/0000-0001-7795-0352), Dept of Biology, Faculty of Science and Engineering, Univ. of Turku, Turku, Finland. – J. Storkey (https://orcid.org/0000-0003-1094-8914), Sustainable Agricultural Sciences, Rothamsted Research, Harpenden, Hertfordshire, UK.

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A major challenge in ecology is to understand how populations are affected by increased climate variability. Here, we assessed the effects of observed climate variability on different organismal groups (amphibians, insects, mammals, herbaceous plants and reptiles) by estimating the extent to which interannual variation in the annual population growth rates (CV_λ) and the absolute value of the long-term population growth rate ($|\log \lambda|$) were associated with short-term climate variability. We used empirical data (≥ 20 consecutive years of annual abundances) from 59 wild populations in the Northern Hemisphere, and quantified variabilities in population growth rates and climatic conditions (temperature and precipitation in active and inactive seasons) calculated over four- and eight-year sliding time windows. We observed a positive relationship between the variability of growth rate (CV_λ) and the variability of temperature in the active season at the shorter timescale only. Moreover, $|\log \lambda|$ was positively associated with the variability of precipitation in the inactive season at both timescales. Otherwise, the direction of the relationships between population dynamics and climate variability (if any) depended largely on the season and organismal group in question. Both CV_λ and $|\log \lambda|$ correlated negatively with species' lifespan, indicating general differences in population dynamics between short-lived and long-lived species that were not related to climate variability. Our results suggest that although temporal variation in population growth rates and the magnitude of long-term population growth rates are partially associated with short-term interannual climate variability, demographic responses to climate fluctuations might still be population-specific rather than specific to given organismal groups, and driven by other factors than the observed climate variability.

Keywords: climate variability, demography, lifespan, long-term time series, organismal group, population dynamics, population growth rate, timescale

Introduction

Global climate change is likely to lead to concomitant changes in climate means, variability and extremes, resulting in more variable and unpredictable environments for animal and plant populations. The consequences of changes in climate means

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for ecological and evolutionary processes have been extensively studied during the past few decades, with the general conclusion being that shifts in mean temperature and precipitation have the ability to alter population fluctuations (reviewed by Walther et al. 2002, Parmesan and Yohe 2003, Oliver and Morecroft 2014). More recently, climate variability (Lawson et al. 2015, Vázquez et al. 2015) and extremes (Palmer et al. 2017, van de Pol et al. 2017) have received increasing attention as important factors that can mediate the effects of shifts in climate means (Vasseur et al. 2014, Lawson et al. 2015). Over the last three decades, variability in regional year-to-year temperature has changed substantially worldwide. For example, in the Northern Hemisphere, especially in North America and Europe, variability in temperature increased notably in the 1980s and 1990s (Huntingford et al. 2013) and extreme temperature events are expected to be even more frequent in the future (IPCC 2014). Moreover, precipitation variability, including precipitation extremes, is predicted to increase in the warmer future climate (IPCC 2014, Pendergrass et al. 2017). Such interannual climate variability has the potential to translate into fluctuations in the abundances of wild populations through changes in individuals' vital rates, such as survival, growth and fecundity (van de Pol et al. 2010, Genovart et al. 2013, Jenouvrier et al. 2015). This link between climate variability and population fluctuations is based on the fact that, for many species, population growth rates are sensitive to shifts not only in the means of vital rates, but also in their variance (Doak et al. 2005, Morris et al. 2008, Vázquez et al. 2015). A major aim in ecology is thus to determine how climate variability can affect populations (Lawson et al. 2015).

One way of measuring population fitness is with the long-term population growth rate, which is a function of annual finite rates of increase (Lewontin and Cohen 1969). Environmental variability is often assumed to decrease the long-term population growth rate (Lewontin and Cohen 1969, Tuljapurkar 1982), thus being harmful for populations. However, previous theoretical and empirical studies have shown that an adverse effect of climate variability on the population growth rate is not a foregone conclusion (Doak et al. 2005, Drake 2005, Koons et al. 2009, Vázquez et al. 2015). Specifically, climate variability can either increase or decrease the long-term population growth rate depending on a species' life history and the vital rates affected (Boyce et al. 2006, Lawson et al. 2015, Colchero et al. 2019), as well as on the mean climatic conditions encountered by the population (Bozinovic et al. 2011, García-Carreras and Reuman 2013). As an example, lifespan is generally expected to be a good predictor of the sensitivity of species to climate variability across diverse taxa, with short-lived species showing greater responses to variations in vital rates than long-lived species are (Morris et al. 2008, Koons et al. 2009, Dalgleish et al. 2010).

So far, many studies have explored the effect of climatic variation on populations by theoretically perturbing vital rates and assuming that all vital rates experience similar proportional changes (Morris et al. 2008, Dalgleish et al. 2010, Jonzén et al. 2010, van de Pol et al. 2010, but see Palmer et al. 2017). However, such theoretical perturbations may not reflect the actual changes in vital rates. Instead, a more direct way to assess the consequences of ongoing climate change for wildlife is to examine the actual responses of wild populations to climate variability. Here, we used data of population abundances ($\geq$ 20 consecutive years) from 11 countries to investigate the effect of short-term interannual climate variability on different organismal groups (amphibians, insects, mammals, herbaceous plants and reptiles) based on 59 wild populations belonging to 54 species. We limited the study to terrestrial, non-migratory species in the Northern Hemisphere (western Europe and North America), where the timing of climate seasonality for populations is mostly synchronized. We sought to determine which organismal groups (if any) were particularly sensitive to the observed climatic variability. We characterized the interannual variability in annual population growth rate as coefficient of variation (CV), and interannual climate variability using average temperature and precipitation in the fall–winter and spring–summer seasons (the inactive and active seasons, respectively). Although we do not expect that these two climate variables would be equally important to all organismal groups, we consider them biologically meaningful for the terrestrial species included here (Post and Stenseth 1999, Deguines et al. 2017, Mills et al. 2017). All variability was quantified within four-year and eight-year moving time windows. More specifically, we focused on the relationships between 1) climate variability and the temporal variation in the observed annual population growth rates (CV_λ), as well as 2) climate variability and the absolute value of the long-term population growth rate ($|\log \lambda|$). The use of $|\log \lambda|$ enabled us to assess the magnitude of population responses to environmental variability regardless of direction because both negative and positive responses are possible (Lawson et al. 2015). As environmental fluctuations can lead to population fluctuations (Tuljapurkar 1982), we predicted that we would find a positive relationship between climate variability and CV_λ, and between climate variability and $|\log \lambda|$ (i.e. we predicted to find an environmental signal in population dynamics). However, because the species included in this comparative study represent diverse life histories, we hypothesized that the effects of the climate variables considered would vary among organismal groups and/or lifespans. Particularly, we predicted that the relationships between the climate variables and two population metrics (CV_λ, $|\log \lambda|$) would be more pronounced for short-lived organismal groups (e.g. insects), which have been reported to be more sensitive to environmental variability than longer-lived species (Morris et al. 2008). As a consequence, the populations of short-lived species would either decline or increase at a higher rate than those of longer-lived species relative to climate variability.

Methods

Population and climatic data collection

Time series on population abundances (either annual population densities or population counts) were extracted from two global databases, the NERC Imperial College Global Population Dynamics Database (GPDD; Prendergast et al. 2010) and the living planet index (LPI; Collen et al. 2009), based on two main criteria. First, demographic data came from non-migratory, terrestrial species located in the Northern Hemisphere (Fig. 1) and consisted of at least 20 consecutive years (selected data were updated when possible using recently published sources; a list of all data sources can be found in the Supporting information). By restricting our analysis to such long-term time series, we hoped to have sufficient information to assess relationships between population dynamics and climate variables (Teller et al. 2016). Second, only wild, unmanaged populations were considered (e.g. harvest data were removed; cf. the Supporting information for further details about criteria). Moreover, we included a subset of weed data from the Broadbalk experiment (Moss et al. 2004) which consisted of the annual frequencies of 19 weed species monitored for 21 years between 1991 and 2014 (three years of data were missing when the plots were fallowed; see Supporting information for details). To find more studies, we also conducted a literature search in July 2018 in the Web of Science using the following search term combinations: (population) AND (demograph*) AND (abundance OR density OR population size OR number) AND (time series OR monitoring) AND (long-term). This search produced 615 matches, of which eleven studies met our selection criteria. Overall, a total of 59 population time series were analyzed; these represented 54 species with different life histories, including 4 amphibian, 6 insect, 20 mammal, 22 herbaceous plant and 7 reptile populations from 28 locations across Europe and North America. The mean length of the studies was 26.2 ± 8.4 years, with the study periods ranging from 1939 to 2016. However, for nine populations representing three different species, we omitted the first 2–19 years to match population abundances with climate data which were available since 1958 (see below and Supporting information for details). Estimates of species' lifespans were obtained from PanTHERIA (Jones et al. 2009), AnAge (<http://genomics.senescence.info/species/>), Animal Diversity Web (ADW (<http://animaldiversity.org/>), Ecoflora (<http://ecoflora.org.uk/>) and peer-reviewed literature (Supporting information). These estimates were often maximum observed or estimated lifespans, which we averaged across different references when possible. The sensitivity of the model results to changes in lifespan estimates was explored separately; the results were found to be robust to uncertainty in lifespan estimates (Supporting information).

For each study location, we extracted monthly gridded values of two key climate variables – temperature (°C) and precipitation (mm month^{-1}) – at a high spatial resolution (~ 4 km, 1/24°) from the TerraClimate dataset (Abatzoglou et al. 2018). Both of these climate variables have been found to affect population dynamics of most of the organismal groups considered here (Post and Stenseth 1999, Deguines et al. 2017, Mills et al. 2017) and therefore, we chose to use the same climate variables for all organismal groups. From these climate data, we derived values for the six-month average of temperature and precipitation for the periods April–September and October–March. In the Northern Hemisphere, these two periods correspond to the active growing season (spring–summer) and the non-active season (fall–winter), respectively, with each period reflecting different environmental conditions. Although less-studied than climatic conditions during the active growing season, changes in winter climatic conditions can also influence the survival, overwintering success and performance of individuals during the following growing season, which can ultimately affect the population growth rate and its variability (Roland and Matter 2013, Williams et al. 2015).

Figure 1. Locations of the 59 study populations included in the dataset. Note that each location may contain multiple populations.

Estimating demographic and climate variability

For each time series, we calculated the observed annual population growth rate (λ) from year t to year $t+1$ as N_{t+1}/N_t, where N denotes population abundance. For the weeds, annual observations were missing for three distinct years in each time series and therefore, we adjusted the growth-rate estimates by the length of the census interval (Morris and Doak 2002, p. 68). We used the coefficient of variation (CV) as our measure of temporal variability in annual population growth rates and in the variability of precipitation to compare the relative amounts of variation across populations and variables that have different means. For the temporal variability of temperature, an interval scale variable, standard deviation was used as a metric of variability. The interannual SD of temperature (SD_{Temp}) and the interannual CV of precipitation (CV_{Prec}) were estimated separately for both active and inactive seasons after detrending the data for each population to remove variation attributable to a long-term temporal trend. The temporal trend was removed by regressing each climatic variable (mean temperature and mean precipitation using a four and eight-year time windows) against year; the residuals of the models were then used to calculate SD_{temp} and CV_{prec}, respectively. CV_{λ} was also estimated after detrending the population growth rate time series. To ease comparison among populations experiencing different climatic conditions, the climate variables (mean, CV and SD) were centered and scaled to have a mean of zero and standard deviation of one for each population time series. Moreover, to describe population dynamics in a variable environment and population responses to climate variability, we calculated the long-term population growth rate (log λ) as the arithmetic mean of the logged annual population growth rates (Morris and Doak 2002) and considered the absolute values of log λ. That is, we focused on change in population size regardless of its direction. Examining log λ per se across multiple species is not informative for our purpose because the direction of the relationship between climate variability and log λ varies within species depending on both the shape of the population response curve and the mean climatic conditions encountered (Lawson et al. 2015). For example, temperature variability enhances the population growth rate of the fruit fly *Drosophila melanogaster* at a low mean temperature, but decreases it at a high mean temperature (Bozinovic et al. 2016). Consequently, if populations in different organismal groups in the present dataset happened to represent contrasting environmental conditions, negative and positive responses could cancel each other out, resulting in no overall response when assessed based on log λ, while this can be avoided using |log λ|.

We then examined the effects of climatic variability on the variation in the annual population growth rates (CV_{λ}) and the absolute value of the long-term population growth rate (|log λ|) within both four-year and eight-year periods. The four-year time window was chosen because a short timescale may better reflect temporal climate variability that is relevant to populations (when high local variations are more pronounced, e.g. extreme events; van de Pol et al. 2017). In the present study, the four-year time window enables multiple observations per population, capturing periods of lower and higher climatic variation during the study period (≥ 20 years) at each location. The eight-year time window, in turn, was chosen as a reference to present longer time periods that might be more relevant to longer-lived organisms. For both sliding time windows, the starting year was moved forward one year at a time to estimate CV_{λ}, |log λ|, SD_{Temp} and CV_{Prec}. The coefficient of variation was corrected for bias in small sample size as following: $\left(1+\frac{1}{4n}\right)\times \mathrm{CV}$, where n refers to the number of records from the time period considered (e.g. $n=4$ for the CVs of climatic conditions estimated over the period of four years; Sokal and Rohlf 1995). In those few cases where an annual estimate of λ was missing (weed time series), the climate variables were adjusted to a five-year (or nine-year) time period.

Statistical analysis

To explore whether climate variability explained a significant proportion of variation in CV_{λ} (sqrt-transformed) or |log λ| (sqrt-transformed), we fitted linear mixed-effects models by including several covariates to control for environmental conditions and spatial heterogeneity. For both analyses and for each season (active and inactive), our full model included CV_{Prec}, SD_{Temp}, organismal group (amphibians, insects, mammals, herbaceous plants, reptiles), species' lifespan (a continuous variable), mean temperature and mean precipitation (in the active or inactive season), latitude, and longitude as fixed effects. Moreover, two-way interactions between the climate variabilities and organismal group, and between the climate variabilities and lifespan were also specified (the full models in Table 1 and Supporting information). In addition, population status (increasing or declining over a given four-year or eight-year time period) as well as the two-way interactions between the climate variability variables (CV_{Prec}, SD_{Temp}) and population status were included in the full model for the analysis of |log λ|. Population ID was included in all models as a random effect. In all statistical analyses, the continuous explanatory variables (covariates) were rescaled: they were centered and standardized to ease model interpretation. Multicollinearity was checked for all climatic variables calculated in the active and inactive seasons and for the variables of each full model using the coefficient of correlation and variance inflation factors (Zuur et al. 2009). We also visually tested for spatial autocorrelation in the residuals of the linear mixed models (Zuur et al. 2009) and found none. All models included a first-order autoregressive correlation structure to account for temporal pseudoreplication (details for model selection in the Supporting information).

For each analysis, model selection was performed based on the Akaike's information criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). As a general approach, we started model selection from the full model (Supporting information) by testing for all two-way

Table 1. Model selection table for the temporal variability in the annual population growth rates (CV_{λ}) and the absolute value of the long-term population growth rate ($|\log \lambda|$) calculated over a four-year sliding time window. Linear mixed-effects models were fitted using a first-order autoregressive structure and population ID (Pop.ID) was treated as a random effect. Climatic mean and variability variables in the active and inactive seasons were investigated separately. The best models ($\Delta AICc < 2$, in italics) and the full model (M_{Full}) are presented with corresponding df (number of parameters), AICc (Akaike's information criterion) and ΔAICc. See the Supporting information for the full model selection.

Name	df	AICc	ΔAICc	Model description
	CV_{λ} – active season			
M1	*17*	*−206.63*	*0.00*	*$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+CV_{Prec}:group$*
M2	*16*	*−206.45*	*0.18*	*$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+CV_{Prec}:group$*
M3	*18*	*−204.93*	*1.70*	*$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+CV_{Prec}:group$*
M4	*23*	*−204.81*	*1.82*	*$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+SD_{Temp}:group+CV_{Prec}:group$*
M5	17	−204.75	1.87	$group+lifespan+longitude+SD_{Temp}+CV_{Prec}+mean_{Temp}+CV_{Prec}:group$
M_{Full}	25	−200.67	5.96	$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}:group+SD_{Temp}:group+CV_{Prec}:lifespan+SD_{Temp}:lifespan$
	CV_{λ} – inactive season			
M1	*7*	*−205.15*	*0.00*	*$lifespan+longitude+mean_{Prec}$*
M2	*8*	*−203.79*	*1.37*	*$lifespan+longitude+mean_{Prec}+mean_{Temp}$*
M3	*8*	*−203.77*	*1.39*	*$lifespan+longitude+mean_{Prec}+SD_{Temp}$*
M4	*8*	*−203.33*	*1.83*	*$lifespan+longitude+mean_{Prec}+latitude$*
M5	*8*	*−203.18*	*1.97*	*$lifespan+longitude+mean_{Prec}+CV_{Prec}$*
M_{Full}	25	−187.86	17.29	$CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}:group+SD_{Temp}:group+CV_{Prec}:lifespan+SD_{Temp}:lifespan$
	$|\log \lambda|$ – active season			
M1	18	−286.04	0.00	$CV_{Prec}+SD_{Temp}+group+status+lifespan+longitude+mean_{Temp}+CV_{Prec}:group$
M_{Full}	28	−277.67	6.31	$CV_{Prec}+SD_{Temp}+group+status+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}:group+SD_{Temp}:group+CV_{Prec}:lifespan+SD_{Temp}:lifespan+SD_{Temp}:status+CV_{Prec}:status$
	$|\log \lambda|$ – inactive season			
M1	*12*	*−286.05*	*0.00*	*$CV_{Prec}+group+status+lifespan+longitude$*
M_{Full}	28	−267.71	15.21	$CV_{Prec}+SD_{Temp}+group+status+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}:group+SD_{Temp}:group+CV_{Prec}:lifespan+SD_{Temp}:lifespan+SD_{Temp}:status+CV_{Prec}:status$

CV_{Prec} = precipitation coefficient of variation during a given season (scaled per population); SD_{Temp} = temperature standard deviation during a given season (scaled per population); $mean_{Prec}$ = mean precipitation during a given season (scaled per population); $mean_{Temp}$ = mean temperature during a given season (scaled per population); group = organismal groups (amphibians, insects, mammals, herbaceous plants and reptiles); status = population status (increasing or declining) in a given four-year time period.

interaction terms, and then used the most-parsimonious model to test for the main effects. If multiple models were equivalent (i.e. $\Delta AICc < 2$), we chose the simplest model based on the principle of parsimony (Table 1, 4, the full model selection in the Supporting information). To describe the proportion of variance explained by the fixed factors, we calculated marginal R^2 values from the final simplified models which best inferred our results (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017). Models were fitted with the *nlme* package (Bates et al. 2015, Pinheiro et al. 2017) in R 4.0.2 (<www.r-project.org>).

Results

Climate variability and CV_{λ}

In both active and inactive seasons, species' lifespan was negatively associated with CV_{λ}, regardless of the timescale, indicating higher temporal variability in annual population growth rates for short-lived species than for long-lived species (Table 1, 2, 4, Fig. 2a – note that in Fig. 2a, the high values of CV_{λ} when lifespan = 30 represent a single population of eastern box turtles). Longitude was a significant covariate in both models (Table 2, 4). Using a four-year sliding time window, SD_{Temp} in the active season correlated positively with CV_{λ} across populations (Table 2, Fig. 2b), suggesting that the annual population growth rate fluctuated slightly more under variable than under stable climatic conditions. Moreover, the relationship between CV_{Prec} and CV_{λ} differed between taxa as indicated by a significant interaction between CV_{Prec} and organismal group in the active season (Table 2). CV_{λ} tended to increase with increasing CV_{Prec} for herbaceous plants and reptiles, while it decreased for amphibians; insects and mammals were less responsive to CV_{Prec} (Table 2, Fig. 2c). During the inactive season, no relationship between climatic variability and CV_{λ} was detected, but CV_{λ} did increase slightly with increasing mean precipitation (Table 2). Using an eight-year time window, no relationship between climatic variability (SD_{Temp}/CV_{Prec}) and CV_{λ} was observed at either of the seasons (Table 4, Supporting information).

Climate variability and $|\log \lambda|$

The absolute value of the long-term population growth rate, $|\log \lambda|$, declined with increasing lifespan and with increasing longitude at both timescales (Table 3, Supporting information). In the active season, the relationship between CV_{Prec} and $|\log \lambda|$ within a four-year time window differed between organismal groups, with particularly insects exhibiting a positive association and mammals a negative association between these two variables (Table 3, Fig. 3). Conversely, using an eight-year time window, $|\log \lambda|$ among insects decreased with higher variability in temperature (SD_{Temp}) in the active season. In the inactive season, CV_{Prec} was marginally positively associated with $|\log \lambda|$ across populations using both sliding time windows (Table 3, Supporting information). Moreover, $|\log \lambda|$ tended to differ among organismal groups, being lower on average for mammals and herbaceous plants than for insects (Table 3). In all analyses, the variation in $|\log \lambda|$ was higher when the population declined over given four- and eight-year

Table 2. Results from the simplified mixed models that best explained the interannual variability in population growth rates (CV$_{\lambda}$ – using a four-year sliding time window) across taxa (n = 59 populations from the Northern Hemisphere). All continuous variables were scaled based on detrended data. The estimates, the 95% confidence intervals (95% CI) and marginal R^{2} values (conditional R^{2} in brackets) are presented (from model M2 and M1 for the active and inactive seasons, respectively, in Table 1).

	Estimate	95% CI	Intercept	Residual	R^{2}
	Active season				
Fixed factors					
Intercept	0.54	[0.37, 0.72]			
Group$_{\text{[Insects]}}$	0.04	[−0.20, 0.28]			
Group$_{\text{[Mammals]}}$	−0.03	[−0.22, 0.16]			
Group$_{\text{[Herb. plants]}}$	−0.01	[−0.21, 0.18]			
Group$_{\text{[Reptiles]}}$	0.13	[−0.11, 0.36]			
Lifespan	−0.12	[−0.19, −0.06]			
Longitude	−0.09	[−0.15, −0.04]			
SD$_{\text{Temp}}$	0.02	[0.01, 0.04]			
CV$_{\text{Prec}}$	−0.05	[−0.11, 0.003]			
CV$_{\text{Prec}}$: Group$_{\text{[Insects]}}$	0.05	[−0.02, 0.12]			
CV$_{\text{Prec}}$: Group$_{\text{[Mammals]}}$	0.05	[−0.01, 0.11]			
CV$_{\text{Prec}}$: Group$_{\text{[Herb. plants]}}$	0.09	[0.02, 0.15]			
CV$_{\text{Prec}}$: Group$_{\text{[Reptiles]}}$	0.09	[0.02, 0.15]			
Random factors					
Pop.ID			0.15	0.24	0.15 (0.38)
	Inactive season				
Fixed factors					
Intercept	0.55	[0.50, 0.59]			
Lifespan	−0.10	[−0.15, −0.05]			
Longitude	−0.08	[−0.13, −0.03]			
Mean$_{\text{Prec}}$	0.02	[0.01, 0.04]			
Random factors					
Pop.ID			0.15	0.25	0.12 (0.36)

time periods (Table 3, Supporting information). However, the relationship between climatic variability and $|\log \lambda|$ was not strongly affected by population status (Table 1, 4, Supporting information).

Discussion

For the five organismal groups considered (amphibians, insects, mammals, herbaceous plants, reptiles) from the Northern Hemisphere, we found some support for our first hypothesis that climate variability translates into temporal variation in the annual population growth rates (CV$_{\lambda}$) and, to a lesser extent, into changes in the absolute value of the long-term population growth rate $|\log \lambda|$. We detected a positive relationship between CV$_{\lambda}$ and SD$_{\text{Temp}}$ across populations in the active season, using a four-year time window only. Moreover, for herbaceous plants, CV$_{\lambda}$ increased with the increasing variability of precipitation in the active season. Our second hypothesis of a positive relationship between climate variability and the two population metrics (CV$_{\lambda}$, $|\log \lambda|$) particularly for short-lived species was not supported; we observed no interaction between the climate variability and lifespan regarding $|\log \lambda|$ or CV$_{\lambda}$ at both timescales. Overall, our results suggest that different organismal groups were weakly affected by the observed climate variability during the study period.

Climate variability and CV$_{\lambda}$

In the present study, inferences about the effect of climate variability on population fluctuations partially depended on the season and timescale, with the active and inactive seasons, and four- and eight-time windows, yielding different outcomes. When the effect of climate variability was assessed based on the active season, variation in temperature was weakly positively associated with CV$_{\lambda}$, using a four-year time sliding window. We also found that CV$_{\lambda}$ for herbaceous plants and reptiles slightly increased with increasing CV$_{\text{Prec}}$ in the active season. These findings were thus in line with our predictions. In the inactive season, we did not find any significant association between climate variability and population fluctuations. The discrepancy between the two seasons might be due to the greater importance of environmental conditions on populations during the active season. Our results indicate that, particularly for herbaceous plant populations, increasing climatic variability might increase their vulnerability to other sources of variation in biotic and abiotic factors (although we did not detect an effect on their $|\log \lambda|$). Importantly, fluctuations in the annual population growth rate may increase the risk of population extinction (Morris and Doak 2002). Contrary to our expectations, we also found a negative relationship between CV$_{\lambda}$ and CV$_{\text{Prec}}$ for amphibians. This result diverges from that reported previously in a meta-analysis for amphibians in the Northern

Table 3. Results from the simplified mixed models that best explained the variability in the absolute value of the long-term population growth rate (|log λ|, using a four-year sliding time window) across taxa (n = 59 populations from the Northern Hemisphere). All continuous variables were scaled. The estimates, the 95% confidence intervals and marginal R^2 values (conditional R^2 in brackets) of model M1 for the active and inactive seasons (Table 1) are presented.

	Estimate	95% CI	Intercept	Residual	R^2
	Active season				
Fixed factors					
Intercept	0.46	[0.34, 0.58]			
SD_{Temp}	0.01	[−4e-04, 0.02]			
$Group_{[Insects]}$	0.12	[−0.04, 0.29]			
$Group_{[Mammals]}$	−0.08	[−0.22, 0.05]			
$Group_{[Herb.\ plants]}$	−0.05	[−0.19, 0.08]			
$Group_{[Reptiles]}$	0.01	[−0.15, 0.17]			
Lifespan	−0.07	[−0.11, −0.03]			
Longitude	−0.07	[−0.11, −0.03]			
meanTemp	0.01	[−0.001,0.02]			
CV_{Prec}	−0.01	[−0.06, 0.04]			
$Status_{[Positive]}$	−0.06	[−0.08, −0.03]			
CV_{Prec}: $Group_{[Insects]}$	0.04	[−0.02, 0.11]			
CV_{Prec}: $Group_{[Mammals]}$	−0.01	[−0.07, 0.04]			
CV_{Prec}: $Group_{[Herb.\ plants]}$	0.02	[−0.03, 0.08]			
CV_{Prec}: $Group_{[Reptiles]}$	0.04	[−0.03, 0.10]			
Random factors					
Pop.ID			0.11	0.21	0.15 (0.32)
	Inactive season				
Fixed factors					
Intercept	0.46	[0.34, 0.58]			
$Group_{[Insects]}$	0.12	[−0.04, 0.29]			
$Group_{[Mammals]}$	−0.08	[−0.22, 0.05]			
$Group_{[Herb.\ plants]}$	−0.05	[−0.19, 0.08]			
$Group_{[Reptiles]}$	0.01	[−0.15, 0.17]			
Lifespan	−0.07	[−0.11, −0.03]			
Longitude	−0.07	[−0.11, −0.03]			
CV_{Prec}	0.02	[0.01, 0.03]			
$Status_{[Positive]}$	−0.06	[−0.08, −0.03]			
Random factors					
Pop.ID			0.10	0.21	0.14 (0.32)

Hemisphere, in which no significant relationship between yearly rainfall variability and the magnitude of population fluctuations was observed (Marsh 2001). These different findings might be due to heterogeneous responses of individual populations. Climatic conditions, including rainfall and drought conditions, are known to influence population dynamics in many amphibian species, but populations responses to these main climate drivers can be highly heterogeneous in direction and magnitude both among and within taxa (Cayuela et al. 2016, Muths et al. 2017). However, a correlative approach, as used in the present study, may also produce spurious relationships between explanatory variables and the data, particularly if the model is over-parameterized (Knape and De Valpine 2011), or if some of the explanatory variables are strongly correlated (Zuur et al. 2010). Although over-parameterization and collinearity were not likely in our case, the observed negative relationship between variation in precipitation and CV_{λ} for amphibians may still be spurious, and reflect other, non-measured processes that correlate with these climate variables. Indeed, interannual variation in population growth rates results from a complex assortment of causal interactions including both the direct and indirect effects of non-climatic factors, such as habitat (e.g. fragmentation or heterogeneity) and biotic factors (e.g. interspecific competition), which might correlate with climatic conditions (Adler et al. 2012, Mantyka-Pringle et al. 2012, Oliver and Morecroft 2014, Papanikolaou et al. 2017). Using an eight-year sliding time window, climatic variability was not associated with interannual variation in the annual population growth rates. This result highlights the importance of the timescale in estimating population responses to environmental variability. In general, short-term climatic variations might be more relevant to many organisms (e.g. short-lived species) than longer-term climatic variations.

As has been reported in previous studies (García et al. 2008, Morris et al. 2008), we found that short-lived species exhibited more variable growth rates than long-lived species. This higher variation in the annual population growth rates of short-lived species was not, however, due to climatic variability, as we observed no effect on CV_{λ} of interactions between variation in temperature or precipitation and lifespan. The greater degree of population fluctuation found in short-lived species (e.g. insects, small mammals) could be due to other biotic factors, such as the abundance of predators,

Table 4. Model selection table for the temporal variability in the annual population growth rates (CV_λ) and the absolute value of the long-term population growth rate ($|\log \lambda|$) calculated across an eight-year sliding time window. Linear mixed-effects models were fitted using a first-order autoregressive structure and population ID was treated as a random effect. Climatic mean and variability variables in the active and inactive seasons were investigated separately. The best models (ΔAICc < 2, in italics) and the full model (M_{Full}) are presented with corresponding df (number of parameters), AICc (Akaike's information criterion) and ΔAICc. See the Supporting information for the full model selection and estimates.

Name	df	AICc	ΔAICc	Model description
	CV_λ – *active season*			
M1	*7*	*−1852.49*	*0.00*	$\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}$
M2	*8*	*−1851.02*	*1.47*	$\mathit{CV}_{Prec}+\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}$
M3	*8*	*−1850.64*	*1.86*	$\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}+\mathit{mean}_{Prec}$
M_{Full}	25	−1836.62	15.87	$\mathrm{CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}{:}group+SD_{Temp}{:}group+CV_{Prec}{:}lifespan+SD_{Temp}{:}lifespan}$
	CV_λ – inactive season			
M1	*7*	*−1851.78*	*0.00*	$\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}$
M2	*8*	*−1850.52*	*1.26*	$\mathit{lifespan}+\mathit{longitude}+\mathit{CV}_{Prec}+\mathit{mean}_{Temp}$
M3	*8*	*−1850.14*	*1.64*	$\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Prec}+\mathit{SD}_{Temp}$
M4	*8*	*−1849.93*	*1.85*	$\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Prec}+\mathit{mean}_{Temp}$
M_{Full}	25	−1838.94	12.84	$\mathrm{CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+CV_{Prec}{:}group+SD_{Temp}{:}group+CV_{Prec}{:}lifespan+SD_{Temp}{:}lifespan}$
	$|\log \lambda|$ – active season			
M1	*19*	*−1049.84*	*0.00*	$\mathit{CV}_{Prec}+\mathit{SD}_{Temp}+\mathit{group}+\mathit{status}+\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}+\mathit{SD}_{Temp}{:}\mathit{group}+\mathit{CV}_{Prec}{:}\mathit{status}$
M2	*20*	*−1047.9*	*1.94*	$\mathit{CV}_{Prec}+\mathit{SD}_{Temp}+\mathit{group}+\mathit{status}+\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}+\mathit{mean}_{Prec}+\mathit{SD}_{Temp}{:}\mathit{group}+\mathit{CV}_{Prec}{:}\mathit{status}$
M_{full}	28	−1044.36	5.48	$\mathrm{CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+status+CV_{Prec}{:}group+SD_{Temp}{:}group+CV_{Prec}{:}lifespan+SD_{Temp}{:}lifespan+SD_{Temp}{:}status+CV_{Prec}{:}status}$
	$|\log \lambda|$ – inactive season			
M1	*13*	*−1046.45*	*0.00*	$\mathit{CV}_{Prec}+\mathit{group}+\mathit{status}+\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}$
M2	*14*	*−1044.56*	*1.89*	$\mathit{CV}_{Prec}+\mathit{group}+\mathit{status}+\mathit{lifespan}+\mathit{longitude}+\mathit{mean}_{Temp}+\mathit{mean}_{Prec}$
M_{full}	28	−1030.83	15.62	$\mathrm{CV_{Prec}+SD_{Temp}+group+lifespan+longitude+latitude+mean_{Temp}+mean_{Prec}+status+CV_{Prec}{:}group+SD_{Temp}{:}group+CV_{Prec}{:}lifespan+SD_{Temp}{:}lifespan+SD_{Temp}{:}status+CV_{Prec}{:}status}$

The climatic variables are calculated over an eight-year sliding time window. CV_{Prec} = precipitation coefficient of variation during a given season (scaled per population); SD_{Temp} = temperature standard deviation during a given season (scaled per population); $mean_{Prec}$ = mean precipitation during a given season (scaled per population); $mean_{Temp}$ = mean temperature during a given season (scaled per population); group = organismal groups (amphibians, insects, mammals, herbaceous plants and reptiles); status = population status (increasing or declining) in a given eight-year time period.

which may regulate prey population sizes more directly than local weather conditions (Hanski et al. 2001).

Overall, the observed associations between climate variability and population variability were statistically significant but weak, which is not surprising given the diversity of taxa that were included. Indeed, Knape and De Valpine (2011) reported that climate effects on animal populations are often difficult to detect in time-series analyses even for large datasets which contain hundreds of time series. Moreover, we acknowledge the fact that the present study covers a large spatial scale (the Northern Hemisphere), which may even overestimate the magnitude of population responses to climate variability compared to studies conducted in single locations (Elmendorf et al. 2015). However, such a large spatial scale considered should not affect the direction of population response (Elmendorf et al. 2015). As a consequence, our findings on the effects of observed climate variability on different organismal groups should be interpreted qualitatively rather than quantitatively.

Climate variability and |log λ|

Theory predicts that climate variability can translate into changes in the long-term population growth rate (Tuljapurkar 1982), but that the direction of these changes is likely to vary across species, depending on their life history, ecology and demographic status (Boyce et al. 2006, Lawson et al. 2015, Vázquez et al. 2015). For instance, empirical findings have indicated that short-lived species might be more vulnerable to climate variability than long-lived species (Morris et al. 2008, Dalgleish et al. 2010), whereas a previous theoretical study suggests that short-lived species with high reproductive output might actually benefit from environmental variation (Koons et al. 2009). As observed in many ectotherms, populations may also respond in a qualitatively different manner to environmental variability depending on the mean environmental conditions encountered and the geographical location within the species' range (Bozinovic et al. 2011, García-Carreras and Reuman 2013, Vasseur et al. 2014, Lawson et al. 2015). Therefore, we used the absolute value of the long-term population growth rates to assess population responses (regardless of their direction) to climate variability. We hypothesized that the relationship between $|\log \lambda|$ and climate variability would be positive for the species that are most responsive to climate variability, such as shorter-lived species. We also predicted that high climatic variation over a longer time scale (eight years) might be more important for longer-lived organisms. Despite the fact that temperature variability in the active season within four-year time periods was positively associated with temporal variation in annual population growth rates across taxa, this variability did not translate into higher absolute values of the long-term population growth rate, $|\log \lambda|$. In contrast to previous studies that have highlighted the essential role of lifespan in population responses to environmental variability (Morris et al. 2008, Koons et al. 2009, Dalgleish et al. 2010), we observed no such an effect (i.e. the interaction between climate variability and lifespan was not significant) using both a four-year and an eight-year sliding time windows. In other words, changes in the long-term growth rates of both short-lived and long-lived species were similarly associated with realised climate variability considered. We only found a negative relationship

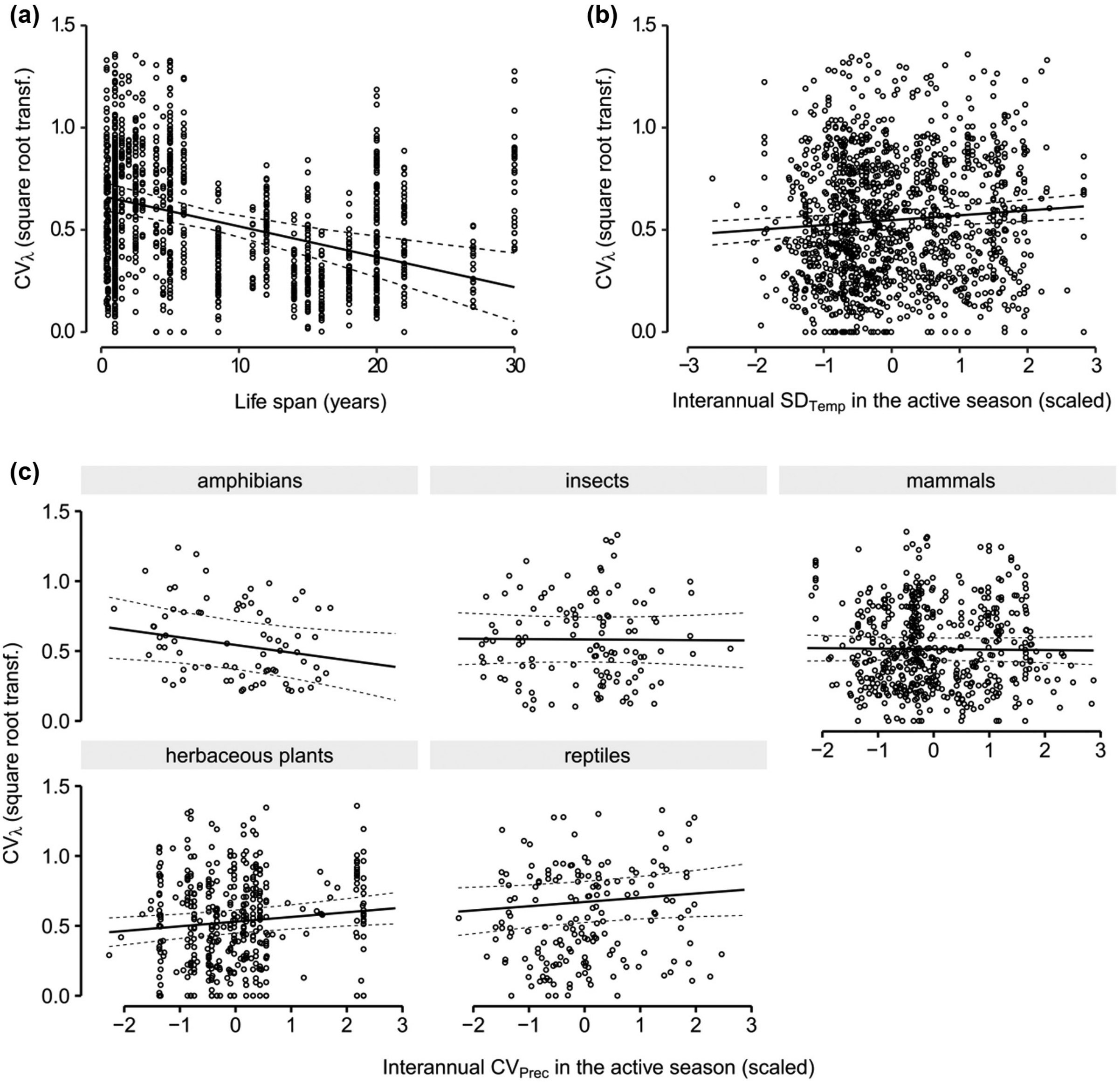

Figure 2. Temporal variability in annual population growth rates (CV_{λ}) calculated across a four-year time window for 59 populations from the Northern Hemisphere and plotted against (a) species' lifespan, (b) variation in temperature (SD_{Temp}) across taxa in the active season and (c) variation in precipitation in the active season (CV_{Prec}) for each organismal group. The fitted lines with 95% confidence intervals are estimated from model M2, Table 1 (CV_{λ} – active season).

between $|\log \lambda|$ and lifespan, suggesting that the populations of short-lived species generally either declined or increased more rapidly than those of longer-lived species. This relationship was moderate over a longer time scale (eight years). However, using a four-year sliding time window, we observed differences in $|\log \lambda|$ in relation to CV_{Prec} in the active season among some organismal groups. The positive relationship between CV_{Prec} and $|\log \lambda|$ of insects, an organismal group involving only short-lived species, suggests that their abundances changed more rapidly when interannual variability in precipitation was high. In the context of climate change, this result indicates that insects might be particularly sensitive to expected changes in climate variability. On the other hand, based on an eight-year timescale, a negative relationship between SD_{Temp} and $|\log \lambda|$ for insects in the active season may question their sensitivity to climate variability. Nevertheless, such a long timescale may be less relevant to insect population dynamics.

Previous comparative studies across taxa are based on hypothetical climate variability and vital rate perturbations (Morris et al. 2008, Dalgleish et al. 2010), while our study relies on true climate variability, which can be smaller than hypothetical variability. Therefore, it is possible that no particular organismal group was heavily affected by the observed climate variability during the past 77 years. This view is also partially supported by a previous study by Palmer et al. (2017), which reported that the responses of 238 British Lepidoptera and bird species to climate variability since

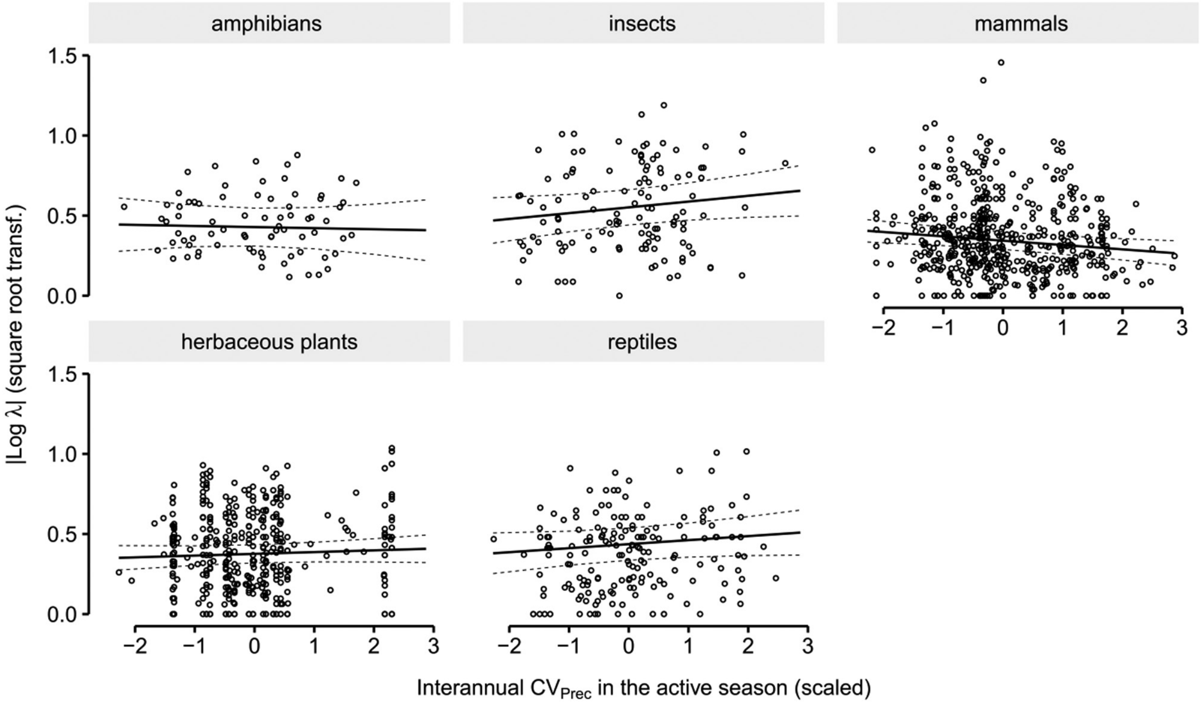

Figure 3. Relationships between the absolute value of the long-term population growth rate (|log λ|) and the variation in precipitation (CV$_{Prec}$) in the active season, for each organismal group considered (based on 59 populations from the Northern Hemisphere). Values are calculated across a four-year sliding time window, the fitted values (black) with 95% confidence intervals are from the linear mixed model M1, Table 1 (|log λ| – active season).

1968 were species-specific. From an evolutionary perspective, adaptation to climate variability via demographic buffering or bet-hedging strategies (Morris and Doak 2004, Nevoux et al. 2010, but see Jongejans et al. 2010) could be partially responsible for the lack of a significant correlation between climate variability and |log λ|. Nevertheless, as we investigated the relationship between climate variability and population responses at the four-year and eight-year time scales only, we cannot rule out the possibility that a different timescale might have revealed a different environmental signal in |log λ|. For instance, changes in the intra-annual variation of climate conditions may also affect population fluctuations and, consequently, population growth rates by modifying the timing of weather conditions and therefore the seasonal abiotic and biotic environments of a population (Shriver 2016, Papanikolaou et al. 2017).

In summary, the present study suggests that temporal fluctuations in population growth rates and the magnitude of long-term population growth rates are partially associated with short-term interannual climate variability, but that these associations may vary depending on the season and organismal groups considered. Species lifespan did not explain sensitivity to observed climate variability in our study. These findings thus indicate that populations might respond individualistically to climate fluctuations and that factors other than the observed climate variability (e.g. density dependence, biotic interactions, local microclimate) are probably more important to the dynamics of wild populations.

Data availability statement

Data supporting the results are available in the GPDD and LPI databases and published sources (detailed in the Supporting information).

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Author contributions

Christie Le Coeur: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Jonathan Storkey**: Data curation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Satu Ramula**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

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